Nature Conservation 31: 17–33 (2018)
doi: 10.3897/natureconservation.31.27407
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Diversity and distribution of food plants: Implications for conservation of the critically endangered Hainan gibbon

Zhidong Zhang[1,2], Runguo Zang[2]

1 *Hebei Provincial Key Laboratory of Forest Trees Germplasm Resources and Forest Protection, College of Forestry, Agricultural University of Hebei, Baoding 071000, China* **2** *Key Laboratory of Forest Ecology and Environment, the State Forestry and Grassland Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Xiangshan Road, Haidian District, Beijing 100091, China*

Corresponding author: *Runguo Zang* (zangrung@caf.ac.cn)

Academic editor: *Christoph Knogge* | Received 13 June 2018 | Accepted 16 November 2018 | Published 18 December 2018

http://zoobank.org/A62399AC-5DE5-440C-AE56-10ADBBF22C98

Citation: Zhang Z, Zang R (2018) Diversity and distribution of food plants: Implications for conservation of the critically endangered Hainan gibbon. Nature Conservation 31: 17–33. https://doi.org/10.3897/natureconservation.31.27407

Abstract

An understanding of the diversity and distribution patterns of Hainan gibbon (*Nomascus hainanus*) foods is essential to its conservation. We used data from plots in various successional stages and *Pinus merkusii* plantations (PF) of Bawangling National Nature Reserve (BNNR) to compare variations in food species diversity and composition amongst forest types. A total of 85 food species and 16,882 food plants individuals were found across forest types. Habitat-exclusive food species were most abundant in old growth natural forest (OGF), followed by mid-aged natural secondary forest (MSF). We did not find exclusive species in PF. For all food species, as well as each stem size class, PF displayed a lower species richness and abundance and, in addition, less similar species composition in each age class compared to secondary forests. The highest stem density and species richness were found in MSF. The abundance of food trees was higher in MSF and OGF than in young natural secondary forest. Results suggested that MSF could serve as an alternative habitat for Hainan gibbons after short-term recovery. Hainan gibbons might be limited to secondary forests older than 25 years old. PF was found to be unsuitable for Hainan gibbons.

Keywords

plant food distribution, conservation management, *Nomascus hainanus*, secondary succession, tropical forests, China

Copyright *Z. Zhang, R. Zang.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Tropical forests are rapidly declining (Steininger et al. 2008) and those remaining are suffering severe damage and fragmentation due to extensive local human activities as well as human-induced global environmental change (Laurance et al. 2011; Zhang et al. 2010). The resulting habitat loss and degradation severely affects forest dwelling animals, especially primates (Arroyo-Rodríguez and Dias 2010; Rode et al. 2006). Habitat conversion from original habitat to highly disturbed habitats is one of the main reasons for the decline in primate populations (Arroyo-Rodríguez and Dias 2010). To effectively conserve the remaining primate populations, extensive knowledge of habitat requirements and resource distribution in fragmented tropical forest landscapes is needed.

The availability of food resources is a main indicator for habitat quality. Changes in food availability are a driving force of changes in primate populations (Mammides et al. 2009; Rode et al. 2006; Worman and Chapman 2006). The density of frugivorous primates is related to the presence of preferred food trees (Worman and Chapman 2006) and influenced by food availability measured as the richness (Mammides et al. 2009) or the density (Mbora and Meikle 2004) of food trees. Other studies of arboreal frugivorous primate species showed that food abundance and distribution also influenced ranging patterns as well as frequency of habitat use (Moscovice et al. 2010; Olupot et al. 1997). Overall, understanding the distribution patterns of food resources and maintaining viable food trees for primates are crucial factors in primate conservation (Mwavu and Witkowski 2009).

Tropical forest succession may be related to the structural and floristic changes, such as changes in plant species richness, stem density and plant species composition (Gibson et al. 2014), which should lead to changes in food resource availability for primates (Bryson-Morrison et al. 2016; Pinotti et al. 2015). The intermediate successional stage is markedly more diverse and abundant than the early stage, but it is not significantly different from the later stage (Kalacska et al. 2004). Tree species composition tends to increase (Kalacska et al. 2004) or changes slightly (Dent et al. 2013) in similarity to old growth forests with forest age. Compared to primary forest, secondary forest is also diverse in terms of primate food species, but large fruit tree are rare (Bryson-Morrison et al. 2016). Understanding which forest types related to different successional stages providing different food resources is vital for the long-term survival of primates.

The Hainan gibbon, *Nomascus hainanus* (Thomas), is the world's rarest ape and one of world's most endangered mammal species (Bryant et al. 2015; Geissmann and Bleisch 2008; Stone 2011; Zhou et al. 2005). The last surviving population (approximately 26 individuals) is confined to the areas of remaining habitat within Bawangling National Nature Reserve (BNNR), on western Hainan Island, China (Deng et al. 2017; Stone 2011). The species is regarded as "Critically Endangered" in the IUCN Red List of Endangered Species due to an estimated population decline of over 80% within the past several decades, primarily resulting from hunting and habitat loss (Geissmann and Bleisch 2008). Since 1989, the Hainan gibbon has been a First Class Nationally Protected Species under the Chinese Wildlife Protection Law (Zhang et al. 2010). The

population was estimated at over 2000 individuals in the 1950s and lived throughout the tropical forest of Hainan Island (Zhou et al. 2005). Deforestation and other anthropogenic activity have led to the species today being restricted to BNNR. Zhou et al. (2005) indicate that the species is unlikely to survive unless efficient conservation policies and strategies are put in place immediately. The apparent threat of extinction that has been known since 2003 led to a series of conservation projects such as reforestation of degraded habitat including planting gibbon food trees that were initiated by local forestry departments, Kadoorie Farm & Botanic Garden (KFBG) and other non-profit organisations (Stone 2011). Although an initial success of the present restoration effort can be seen, basic knowledge regarding the distribution of food trees that are important for Hainan gibbon long-term survival remain unclear (Fellowes et al. 2008).

Accordingly, the overall goal of this study was to assess diversity patterns of food trees and variation in community composition across different successional stages of natural forests, as well as plantations, to improve our understanding of food distribution and succession in BNNR. Our study provided basic information on distribution patterns of food trees species for the Hainan gibbon to ensure the long term conservation and survival of this unique species.

Material and methods

Study area

BNNR (18°57.15'–19°11.21'N, 109°03.32'–109°17.51'E) is located in west Hainan Island, south China (Fig. 1), at the northern edge of the Asian tropical forest zone (Ding et al. 2012). It covers an area of 482 km^2, with its highest peak being 1654 m above sea level (Fig. 1). BNNR was established as a National Nature Reserve in 1988 with the main objective of conserving the Hainan gibbons and their habitat. The region is characterised by a tropical monsoon climate with a distinct wet season from May to October and a dry season from November to April. The average annual precipitation is 1750 mm and average annual temperature is 23.6°C. Soils at higher elevations are mixtures of red loam and yellow loam, while latosol, developed from granite, dominates soils at lower elevations (Zang et al. 2010).

The landscape in BNNR is a mosaic of natural vegetation and exotic species plantations in which natural tropical forests dominate. Due to severe and repeated anthropogenic disturbances over the past 40 years, forest landscapes in BNNR have become increasingly fragmented and old growth forests have been progressively replaced by secondary forests in various development stages, shrub/grass land and rubber or pine plantations (Zang et al. 2010). Logging operations may modify the diet of Hainan gibbons directly by cutting down important food trees and indirectly by transforming original forests into secondary vegetation or plantations (Morgan and Sanz 2007). In summary, it can be said that the past anthropogenic activity in the region has gradually destroyed habitats and food resources for Hainan gibbons (Zhou et al. 2005).

Data collection

Gibbon food trees were defined as tree species whose edible parts (leaves, flowers, fruits or seeds) are known to be part of the gibbon's diet in the area. We used food plant lists from long-term studies of the Hainan gibbons in the tropical forest region of BNNR (Chen et al. 2009; Lin et al. 2006; Wu 2007; Zhou 2008) to identify food plants amongst the surveyed species. We investigated a total of 149 sample plots (20 × 20 m) based on 1 × 1 km or 1 × 2 km grid across the BNNR forest region (Fig. 1). At each grid point, an inventory plot was established and positioned by a hand-held global positioning device (GPS) for the vegetation survey. Sample plots cover a total area of 5.96 ha in four forest types. The forest types were classified based on time since the harvest or the successional stage of the forest was within the period of the inventory. For the classification of successional stages, information available from timber harvest archives of the BNNR was used. In addition, we employed experienced loggers to identify the successional stages in each sample plot. Of the total number of plots, 33 fell within the young natural secondary forests (YSF; < 25 years since disturbance), 26 in middle-aged natural secondary forests (MSF, 25–60 years since disturbance), 76 in old growth forests (OGF, > 60 years since disturbance) and 14 in *Pinus merkusii* plantation forests (PF, 20–35 years).

In each sample plot, all free standing woody stems with diameter at breast height (DBH) ≥ 1 cm, were counted, measured and identified to the species level. Species nomenclature follows Flora of China (http://www.efloras.org). In total, we surveyed 60,930 woody stems belonging to 587 species, 275 genera and 82 families.

Adult trees generally produce a greater quantity of food resources than younger trees (Chapman et al. 1992) and only those trees with a DBH ≥ 10 cm are large enough for Hainan gibbon to forage in, so we used tree DBH as an indicator to determine suitable food trees. Tree DBH is commonly used to describe primate resources (Worman and Chapman 2006). In order to account for differences in species richness and individual density of food tree size classes amongst the four forest types, all woody stems were classified into three size classes: saplings (1 cm ≤ DBH < 5 cm), young trees (5 cm ≤ DBH < 10 cm) and adult trees (DBH ≥ 10 cm).

We treated each plot (20 × 20 m) as a unit for all subsequent analyses, except for the accumulation curves. For each plot, we quantified species richness as well as stem density of all food tree species.

Data analysis

To compare food species diversity amongst the four forest types, we computed sample-based rarefaction curves constructed using the analytical formula implemented in EstimateS 9.0 (Colwell 2013). Rarefaction curves can be used to standardise samples that differ in terms of individual size or plot size. This procedure was repeated for each of the 200 bootstrap iterations. Patterns of species dominance were compared between

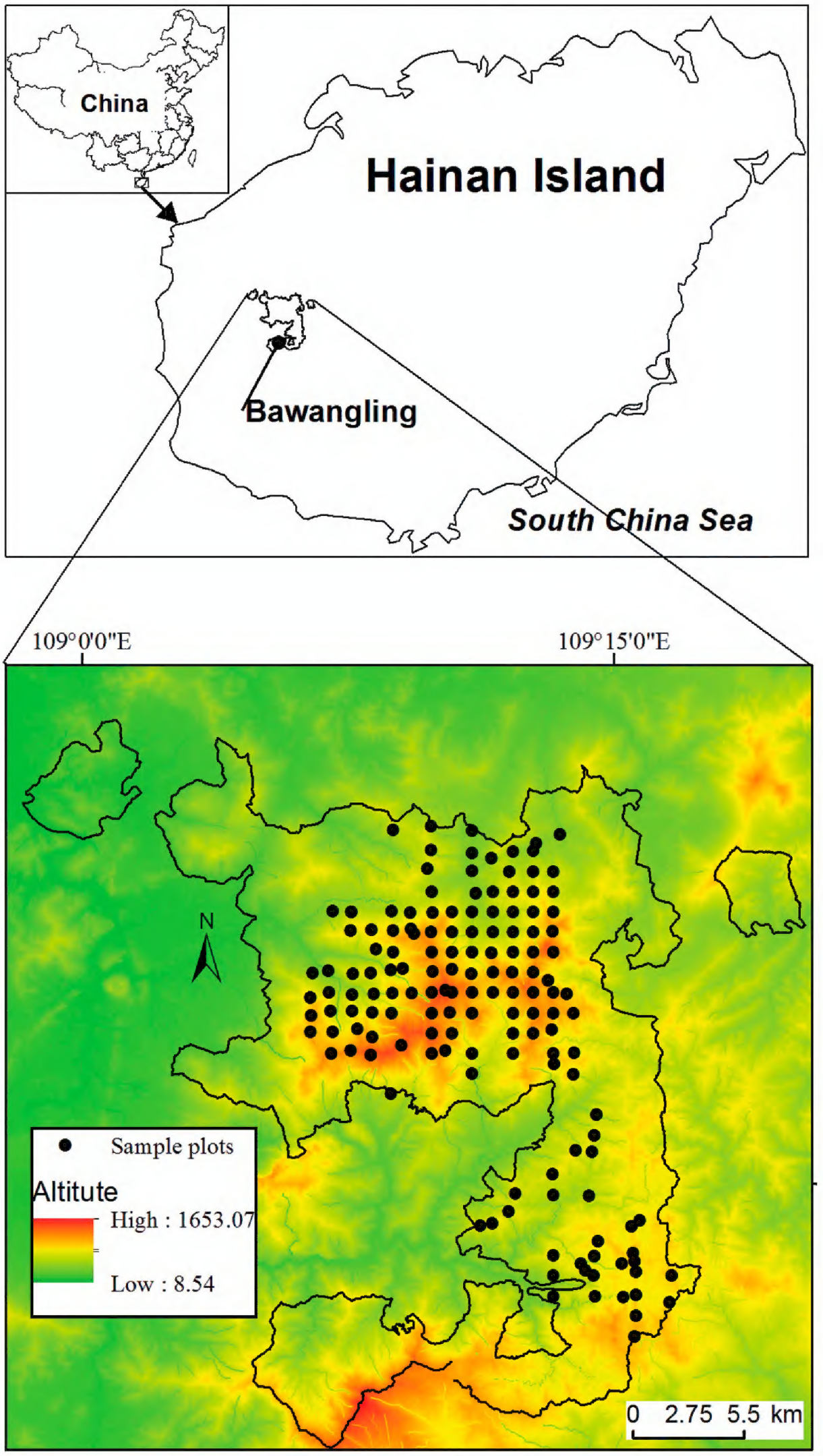

Figure 1. The study area and distribution of sample plots in the tropical forest region of Bawangling National Nature Reserve, Hainan Island, China.

different forest types using species rank-abundance plots. The significance of differences amongst forest types with respect to the food species richness for three stem size classes was assessed by one-way ANOVA, followed by a Tukey HSD multiple comparisons test when significant differences ($p < 0.05$) were found. Prior to the statistical analysis, all data were log-transformed.

We assessed the completeness of each forest type by calculating the number of observed species as a percentage of the total richness and coverage of each forest type by calculating the number of species recorded as a percentage of the average estimated richness, which was estimated based on the average of two abundance-based non-parametric estimators: Chao 2 and jack 2 (Colwell 2013). Both estimators were used to reduce the bias in underestimating species richness and have been shown to be accurate to true species richness relative to other non-parametric estimators, especially when based on small sample sizes (Hortal et al. 2006).

We used ANOSIM (analysis of similarities) to test whether species composition differed amongst four forest types for each DBH size class (saplings, young trees and adult trees) using the ANOSIM function in the Vegan package. ANOSIM was implemented with a maximum of 999 permutations. Pairwise similarities showing community overlay between forest types for each DBH size class were also calculated based on Sørenson's quantitative index (Chao et al. 2005) using the SIM function in the Vegetarian package. All the statistical analyses were performed with R 3.3.2 (R Core Team 2016) unless otherwise indicated.

Results

A total of 85 species belonging to 55 genera in 35 families were identified amongst 16,882 collected food plants (Suppl. material 1: Table S1). The families with the highest number of species were Lauraceae (13%), Moraceae (12%) and Myrtaceae (8%). The most abundant families were Rubiaceae (38%), Lauraceae (12%) and Myrtaceae (6%). Distribution of food tree species amongst forest types was different, ranging from 21 species present in all forest types to 11 species exclusive to one single forest type each (Table 1).

Changes in species diversity patterns

Food trees were at least 70.5% of the estimated total number of species in each forest type (Table 1). This result displays the validity of our comparisons of species richness amongst four forest types. At least 83.5% of all trees were recorded in natural forests with various successional stages, while only 25.9% of all trees were found in plantations. Habitat-exclusive species had the highest richness in OGF, followed by MSF, while we did not find habitat-exclusive species in PF. At plot scale, stem density and species diversity were higher in the natural forests (YSF, MSF and OGF) and the

Table 1. Diversity of total sampled food trees suitable for Hainan gibbon in young secondary forests (YSF), intermediate secondary forests (MSF), old forests (OGF) and plantation forests (PF) of BNNR, Hainan Island, China. N = total number of sampled plots, n = number of individuals sampled, S_{tot} = total number of species recorded, ***Coverage*** = number of species recorded as a percentage of the average estimated richness, S_{plot} = mean richness per plot ± standard error (ANOVA $F_{3,145} = 15.3$, $p < 0.001$), D_{plot} = mean density per plot ± standard error (ANOVA $F_{3,145} = 14.5$, $p < 0.001$), $\hat{S}_{MaoTao}$ = species richness at a standardised sampled size, ***Completeness*** = number of species recorded as a percentage of the landscape total, Ex_{tot} = total number of habitat-exclusive species. Values designated by the different letters within each variable are significant at $p < 0.01$.

Forest type	N	n	S_{tot}	Coverage (%)	D_{plot}	S_{plot}	$\hat{S}_{MaoTao}$ for n=14	Completeness (%)	Ex_{tot}
YSF	33	3707	71	90.2	119.6±16.1a	17.4±1.8bc	62.7±0.8	83.5	1
MSF	26	3683	73	84.1	141.7±15.2a	21.3±1.5c	64.2±0.9	85.9	3
OGF	76	9020	81	96.8	118.7±9.5a	15.1±0.9b	62.7±0.7	95.3	7
PF	14	472	22	70.5	36.3±18.6 b	4.8±0.8a	22±0.6	25.9	0
All	149	16882	85		115.6±7.1	15.8±0.8	62.3±1.1		11

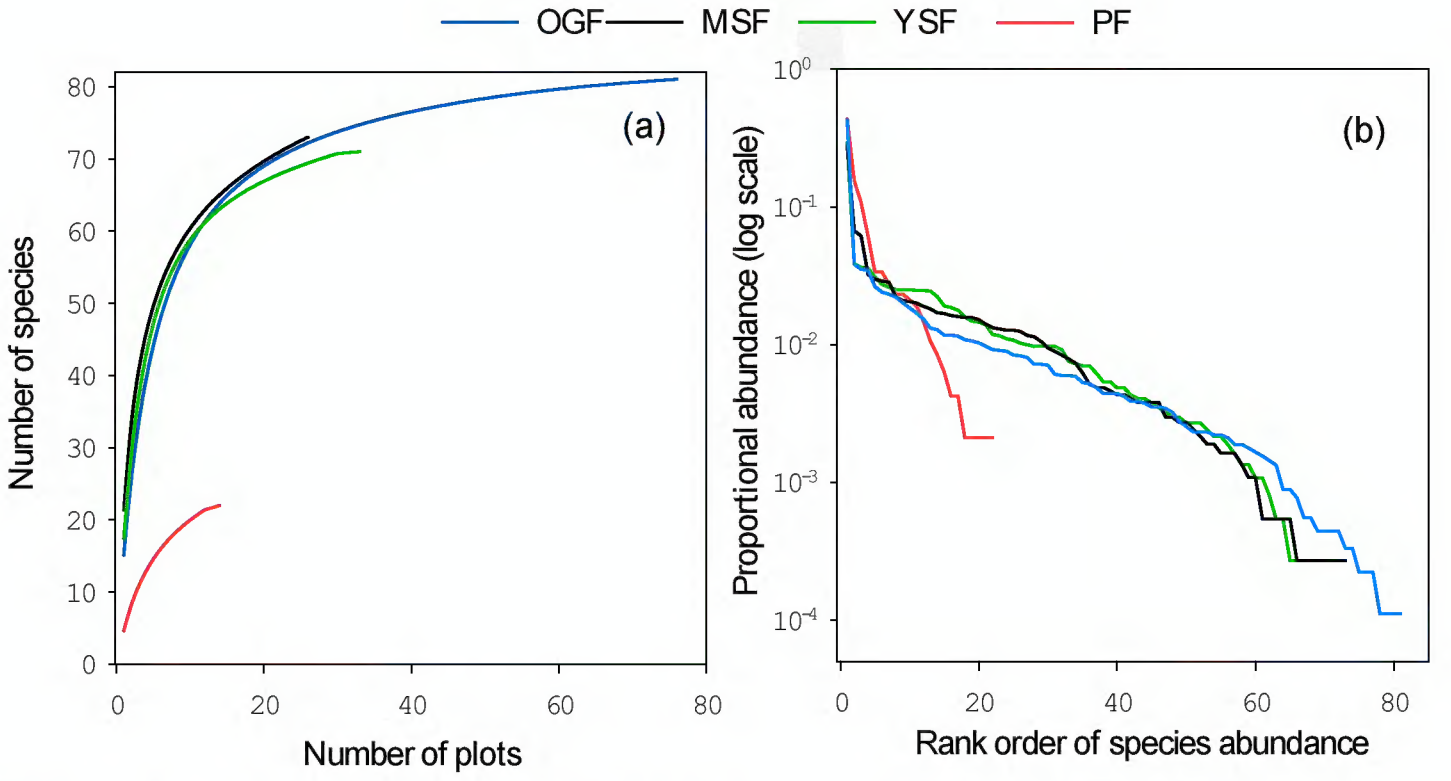

Figure 2. Sample-based rarefaction curves and rank-abundance distribution of all food tree species in young secondary forests (YSF), intermediate secondary forests (MSF), old forests (OGF) and plantation forests (PF).

highest stem density and species richness were found in MSF ($p < 0.01$) (Table 1). The analysis between forest types using a standardised sample size ($\hat{S}_{MaoTao}$ for $N = 14$) showed species richness across four forest types were similar to the plot-scale diversity patterns (Table 1).

Rarefaction curves for all four forest types were nearly asymptotic, with species richness being highest in MSF and lowest in PF (Fig. 2a). Plantations were dominated by a few very abundant species (Fig. 2b). The four dominant species *Psychotria rubra*, *Syzygium chunianum*, *Adinandra hainanensis* and *Machilus chinensis* accounted for

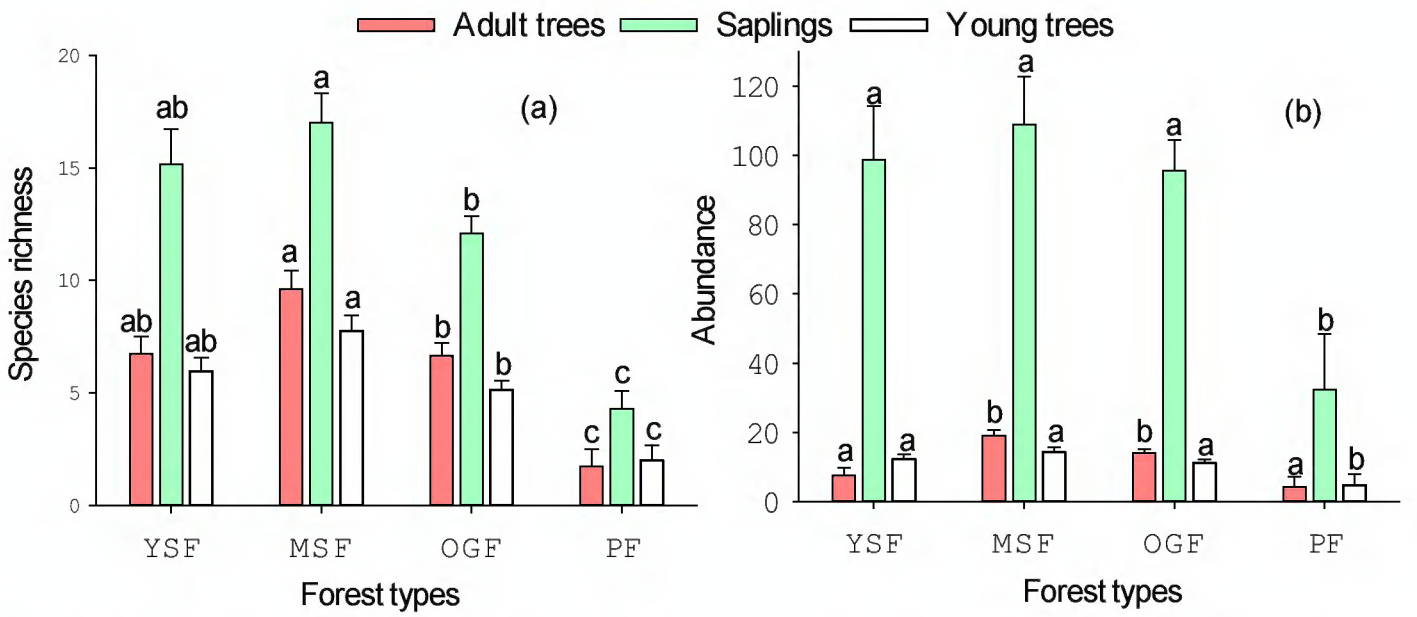

Figure 3. Species richness (**a**) and abundance (**b**) (mean ± standard error) distribution of food tree DBH size classes in young secondary forests (YSF), intermediate secondary forests (MSF), old forests (OGF) and plantation forests (PF). Significant differences ($p < 0.05$) between the units based on Tukey HSD test are indicated using the different letters.

75.8% of the sampled individual trees. Natural forests exhibited lower species dominance than plantations and the differences of species dominance amongst various recovery stages were not significant (Fig. 2b).

There were significant differences amongst forest types regarding species richness and abundance of various DBH size classes ($p < 0.001$ in all cases). All size classes of food trees in plantations displayed significantly lower species richness than each of the three natural secondary forest types (Fig. 3a). MSF showed considerably more food trees richness (Adult: 9.62±0.83; Saplings: 17±1.33; Young: 7.76±0.67) across all size classes per plot compared to OGF (Adult: 6.66±0.57; Saplings: 12.11±0.75; Young: 5.14±0.40). The abundance of adult food trees was higher in MSF (19.08±1.71) and OGF (14.00±1.18) than in YSF (7.57±2.25) and PF (4.25±2.93) (Fig. 3b). No significant differences were found regarding the abundance of saplings and young trees amongst the different forest successional stages ($p > 0.05$). However, saplings and young trees of food species were more prevalent in natural forests (YSF, MSF and OGF) than in PF (Fig. 3b).

Variation in species composition

Differences in species composition amongst forest types were significant for adult trees, young trees and saplings (ANOSIM test, $R > 0.3$, $p < 0.05$ in all cases). Furthermore, pairwise comparisons revealed that PF had distinct species assemblages for all size classes and OGF exhibited strikingly different adult trees (ANOSIM test, $R = 0.27$, $p < 0.05$) or saplings species (ANOSIM test, $R = 0.21$, $p < 0.05$) composition compared to YSF. There was no significant difference in young trees species composition between

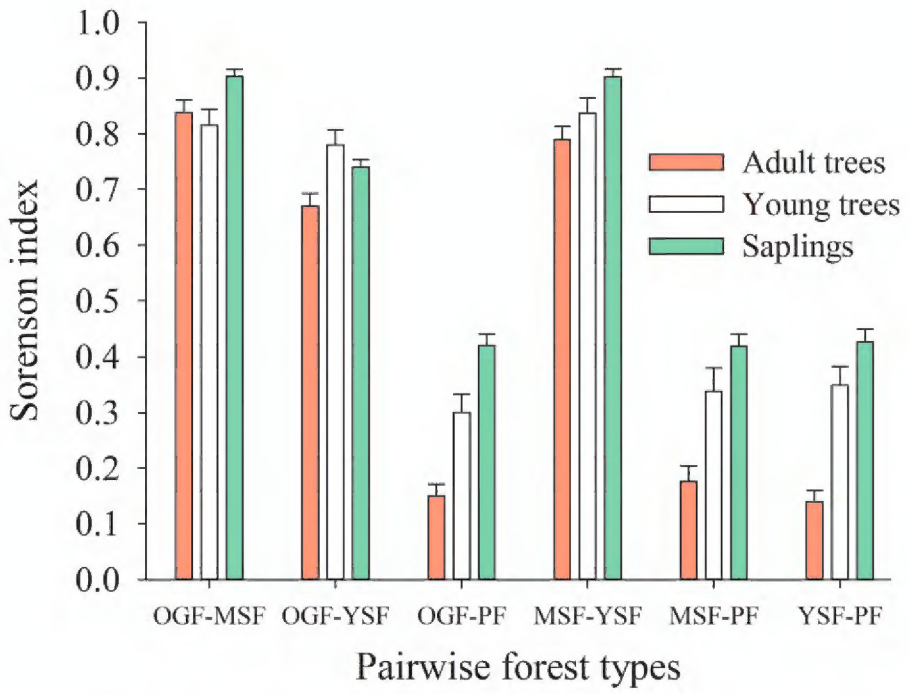

Figure 4. Compositional similarity of food tree DBH size classes amongst young secondary forests (YSF), intermediate secondary forests (MSF), old forests (OGF) and plantation forests (PF) in the study area. Results are shown for Sørenson's quantitative index. Error bars are standard errors, computed by a bootstrapping procedure.

different successional stages of natural forests. Floristic similarity for young trees species was, however, slightly higher between MSF and YSF than between OGF and MSF or between OGF and YSF (Fig. 4).

Discussion

BNNR currently remains the last refuge for Hainan gibbons in the world (Stone 2011). The food tree diversity and composition assessment in the BNNR, presented in this study, highlights distribution patterns amongst different forest types and displays important information for the successful protection and conservation of Hainan gibbons in the future. Food abundance and forest type likely have a stronger influence on primate habitat selection than any other factors (Furuichi and Hashimoto 2004).

Compared to natural forests in different successional stages (YSF, MSF and OGF), plantations (PF) have unfavourable attributes, such as a lack of soil humidity, higher solar radiation, lower litter decomposition rates and a greater density of ruderal species (Lemenih et al. 2004; Lohbeck et al. 2013; Nagaike 2002) that result in lower richness and abundance of food trees, most of which are shade-tolerant species (Table 1, Figs 2a, 3). PF also had a distinct species composition amongst all size classes (adult trees, young trees and saplings) due to the differences in forest structure and the aforementioned characteristics. Different plantation management practices can also affect food tree diversity. The thinning of objective trees in an appropriate period for timber production can efficiently minimise the decrease in the abundance and richness of the food resource, especially shade-intolerant trees (Sakamaki et al. 2011). However,

clear-cutting, most common in BNNR, is likely to reduce the number of food trees and proportion of larger food trees during timber harvesting (Table 1, Figs 2a, 3). In BNNR, planted forests are generally found in the areas below 760 m where anthropogenic disturbances occur more frequently than at higher elevations (Zhang et al. 2010; Zhou et al. 2005). The lack of food resources, lower numbers of large food trees and simple forest structures in plantations have severely limited Hainan gibbon's ability for locomotion, feeding and resting. To date, the gibbons have never been seen in plantations (Zhang et al. 2010). Therefore, converting plantations back into forest, useable by gibbons, is of highest importance.

The development of species diversity along successional gradients may follow this hypothesis: that species diversity increase with vegetation recovery time, but peaks at mid-succession (Auclair and Goff 1971). As expected, a similar pattern of total food species diversity distribution across successional stages was identified in our study as well, regardless of whether or not stem density per plot and the number of species (S_{plot} and $\hat{S}_{MaoTao}$ for $N = 14$) were considered (Table 1, Fig. 2a). Similar results for each DBH size class distribution were also found (Fig. 3). Food species diversity patterns could be explained by trade-offs in dispersal and competitive ability (Howard and Lee 2003). The trade-offs limit species presence at the two successional extremes (YSF and OGF). However, in the mid-successional stage, most tree species have already dispersed and established, but competitive exclusion has not yet eliminated the shade-intolerant food species, resulting in the highest food species diversity. Similarly, the decline in food species diversity in OGF may have resulted from reduced light availability (Lohbeck et al. 2013). As trees become larger, canopy cover becomes denser and low light levels may inhibit food species recruitment from seed or seedling banks, thus limiting food species richness and stems with small DBH class (Fig. 3). Our results could also be explained by the intermediate disturbance hypothesis (IDH), which indicates that species diversity is maximised where intermediate scales of disturbance are experienced (Connell 1978). There may be a trade-off between species' competitive ability and adaptation to disturbance (Mackey and Currie 2001). Habitat conditions at intermediate disturbance levels can maintain the coexistence of competitive species and disturbance-tolerant species. Thus, a peak in diversity should occur at habitats with intermediate disturbance level. Generally, factors to evaluate disturbance levels include frequency, extent, intensity and time since disturbance occurred. Compared to OGF and YSF, MSF had the highest food species diversity due to intermediate disturbance intensities and times since the last disturbance it experienced. BNNR has experienced ca. 40 years of logging by 1994 (Zang et al. 2010). Many large food tree species are valuable timber trees as well (e.g. *Homalium hainanense*, *Castanopsis hystrix*, *Podocarpus imbricatus* et al.) and have therefore been specifically targeted during past harvest operations. As a result, the large food trees preferred by gibbons were lost in young secondary forests and are restricted to primary or old-growth forest adjacent to ravine areas (Liu et al. 1989; Wu 2007). After 25–60 years of succession, the adult food tree diversity increased with recovery age and were equivalent to, or slightly higher than, OGF levels (Fig. 3), suggesting that

prohibition of mechanical logging since 1994 apparently stimulated the growth of large trees that provide food for gibbons.

Our study revealed that differences between OGF and YSF were larger than those between MSF and YSF or between OGF and MSF regarding food species composition in each DBH size class (Fig. 4), indicating that food species composition in secondary forests became more similar to that in old growth with increasing age. Our results showed many similarities to a study by Howard and Lee (2003) on Barro Colorado Island in Panama, where species composition and availability of food resource in secondary forests converged towards those characteristics found in old-growth forests with stand age. This hints at the fact that it is possible to successfully recreate lost habitats. In the tropical forest of north-eastern Costa Rica, Letcher and Chazdon (2009) also found that secondary forests (> 30 years) have similar species composition to the old growth forest. The changes of food species composition across successional gradients may be attributed to the land-use history (Letcher and Chazdon 2009) and conversion of plant strategies from acquisition in the early successional time to conservation in the late successional stage (Lohbeck et al. 2013). Other factors, such as the extent and condition of surrounding forests, can also impact the distribution of species composition (Chazdon 2003). The driving forces influencing food species composition variation, however, need to be further tested based on abiotic factors and measure-based functional traits data in future studies, to ensure a fast and successful conversion of depleted forests back into suitable habitat.

In this study, eleven food tree species were detected exclusively in one single forest type (Table 1). They are very infrequent and an important source of fruits fed on by Hainan gibbons (Chen et al. 2009). For example, *Ficus championii* was identified as one of the preferred food resources for gibbons (Chen et al. 2009; Wu 2007). *Pouteria annanmensis* was consumed in the driest months (February-April). It was reported that there were only seven food species consumed by Hainan gibbons during the dry season (Chen et al. 2009; Liu et al. 1989; Wu 2007), suggesting that the presence of *Pouteria annanmensis* may have helped to improve seasonal resource availability in resource-poor months. OGF had higher habitat-exclusive food species richness (7) than MSF (3) and YSF (1), although the differences of species dominance between various successional stages were not significant. It is crucial to consider these food species, especially in OGF, as a priority for conservation to develop effective management and restoration plans for Hainan gibbons.

Implications for conservation

This study allows informed decision-making regarding what forest types this highly endangered species needs to survive (Tweheyo et al. 2004). At present, suitable forest habitat for Hainan gibbons is fragmented and mainly restricted to a very small region of ca.14–16 km^2 (Zhou et al. 2005). Fellowes et al. (2008) revealed that gibbons frequently forage in narrow strips of habitats adjacent to degraded shrub lands

and monoculture pine plantations. So one promising activity would be to expand the area suitable for the use by gibbons through planting food tree species in shrub-grass lands, old logging tracks and skid rows as well as plantations where food species diversity is currently the lowest (Table 1). Suitable species include those consumed most frequently by the apes such as *Endospermum chinense*, *Bischoffia javanica*, *Polyalthia laui*, *Ficus championii* and *Nephelium topengii* and species which fruit in late winter months when the natural food source is scarce, especially *Schefflera octophylla*, *Ficus altissima*, *Elaeocarpus subglobosus*, *Podocarpus neriifolius* and *Pouteria annanmensis* (Chen et al. 2009; Wu 2007). Other studies have shown that primates prefer primary forest (Fan et al. 2011; Furuichi et al. 2001; Zhang et al. 2010). However, with increasing recovery time, secondary forests may help the survival of Hainan gibbons and improve habitat suitability because of the high density and richness of important adult foods trees (Fig. 3). We believe this approach to be very promising because the preference for certain vegetation types is influenced mainly by the abundance of food resource rather than forest type per se (Furuichi et al. 2001). *Pinus merkusii* plantation forests could also serve as corridors between suitable forest patches or as refuge vegetation for Hainan gibbons if high-quality food species were not removed during low-impact logging or supplemental planting programmes were adopted. Accordingly, future priority actions in BNNR have to be aimed at (1) further protecting large food trees and habitat-exclusive food species in each habitat; (2) promoting recovery and regeneration of natural forest fragments and plantations where most of the important food tree species are associated; (3) implementing special measures (such as directional felling) to avoid damaging food trees and reducing the degree of forest canopy damage so as to preserve important food resources and nesting sites for Hainan gibbons and (4) extending our research to predict the potential distributions of important food tree species and analysing the effect of food availability on Hainan gibbon. Of courses, besides food availability, other factors, such as genetic and anthropogenic factors, are also likely to constrain Hainan gibbon population (Bryant et al. 2016; Bryant et al. 2017) and conservation actions should also focus on managing these factors. If these measures are adopted in the near future, there is a realistic chance that this rare species can survive and remain amongst those species that are characteristic to Hainan Island.

Conclusions

Intermediate secondary forests, which appeared to have a more similar food species composition to old forest and higher adult food species diversity, could serve as an alternative habitat for Hainan gibbons in the short term, given that further anthropogenic disturbances are successfully ruled out. However, Hainan gibbons will find limited resources in secondary forests less than 25 years old, while non-suitable structural characteristics and limited food resources make *Pinus merkusii* plantations unsuitable for Hainan gibbons.

Acknowledgements

This work was financially supported by the Fundamental Research Funds for the National Nonprofit Research Institution of Chinese Academy of Forestry (CAFB-B2017ZB004-01), the National Science Foundation of China (31370636) and the Program of Study Abroad for Young Teachers by Agricultural University of Hebei. We are particularly grateful to the anonymous reviewers and the editor for valuable comments that helped to improve the manuscript.

References

Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72: 1–16. https://doi.org/10.1002/ajp.20753

Auclair AN, Goff FG (1971) Diversity relations of upland forests in the western Great Lakes area. The American Naturalist 105: 499–528. https://doi.org/10.1086/282742

Bryant JV, Gottelli D, Zeng X, Hong X, Chan BPL, Fellowes JR, Zhang Y, Luo J, Durrant C, Geissmann T, Chatterjee HJ, Turvey ST (2016) Assessing current genetic status of the Hainan gibbon using historical and demographic baselines: implications for conservation management of species of extreme rarity. Molecular Ecology 25: 3540–3556. https://doi.org/10.1111/mec.13716

Bryant JV, Turvey ST, Wong MHG, Traylor-Holzer K (2015) Conserving the world's rarest ape: action planning for the Hainan gibbon. Oryx 49: 391–392. https://doi.org/10.1017/S0030605315000563

Bryant JV, Zeng X, Hong X, Chatterjee HJ, Turvey ST (2017) Spatiotemporal requirements of the Hainan gibbon: Does home range constrain recovery of the world's rarest ape? American Journal of Primatology 79. https://doi.org/10.1002/ajp.22617

Bryson-Morrison N, Matsuzawa T, Humle T (2016) Chimpanzees in an anthropogenic landscape: Examining food resources across habitat types at Bossou, Guinea, West Africa. American Journal of Primatology 78: 1237–1249. https://doi.org/10.1002/ajp.22578

Chao A, Chazdon RL, Colwell RK, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8: 148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Chapman CA, Chapman LJ, Wangham R, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. Biotropica 24: 527–531.https://doi.org/10.2307/2389015

Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology Evolution and Systematics 6: 51–71. https://doi.org/10.1078/1433-8319-00042

Chen SH, Yang SB, Xu H, Li YD, Ding Y, Zang RG (2009) Study on edible plants and main plant population structures in distributed area of *Hylobates hainanus*, Bawangling National Nature Reserve, Hainan island, China. Guangdong Forestry Science and Technology 25: 45–51.

Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples. Version 9. http://viceroy.eeb.uconn.edu/estimates [Accessed on 04 August 2016]

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Deng H, Zhang M, Zhou J (2017) Recovery of the critically endangered Hainan gibbon *Nomascus hainanus*. Oryx 51: 161–165. https://doi.org/10.1017/S0030605315000678

Dent DH, DeWalt SJ, Denslow JS (2013) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. Journal of Vegetation Science 24: 530–542. https://doi.org/10.1111/j.1654-1103.2012.01482.x

Ding Y, Zang R, Liu S, He F, Letcher SG (2012) Recovery of woody plant diversity in tropical rain forests in southern China after logging and shifting cultivation. Biological Conservation 145: 225–233. https://doi.org/10.1016/j.biocon.2011.11.009

Fan PF, Fei HL, Scott MB, Zhang W, Ma CY (2011) Habitat and food choice of the critically endangered cao vit gibbon (*Nomascus nasutus*) in China: implications for conservation. Biological Conservation 144: 2247–2254. https://doi.org/10.1016/j.biocon.2011.05.016

Fellowes JR, Chan BPL, Zhou J, Chen SH, Yang SB, Chit NS (2008) Current status of the Hainan gibbon (*Nomascus hainanus*): progress of population monitoring and other priority actions. Asian Primates Journal 1: 2–9.

Furuichi T, Hashimoto C (2004) Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kalinzu forest, Uganda. International Journal of Primatology 25: 755–765. https://doi.org/10.1023/B:IJOP.0000029121.25284.7f

Furuichi T, Hashimoto C, Tashiro Y (2001) Fruit availability and habitat use by chimpanzees in the Kalinzu forest, Uganda: examination of fallback foods. International Journal of Primatology 22: 929–945. https://doi.org/10.1023/A:1012009520350

Geissmann T, Bleisch W (2008) *Nomascus hainnanus*. The IUCN Red List of Threatened Species 2008. e.T41643A10526461. http://www.iucnredlist.org/details/41643/0

Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2014) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–381. https://doi.org/10.1038/nature10425

Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. Journal of Animal Ecology 75: 274–287. https://doi.10.1111/j.1365-2656.2006.01048.x

Howard LF, Lee TD (2003) Temporal patterns of vascular plant diversity in southeastern New Hampshire forests. Forest Ecology and Management 185: 5–20. https://doi.org/10.1016/S0378-1127(03)00243-3

Kalacska M, Sanchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH (2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. Forest Ecology and Management 200: 227–247. https://doi.org/10.1016/j.foreco.2004.07.001

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS, Zartman CE, Boyle SA, Didham RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest fragments: a 32-year investigation. Biological Conservation 144: 56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Lemenih M, Gidyelew T, Teketay D (2004) Effects of canopy cover and understory environment of tree plantations on richness, density and size of colonizing woody species in southern Ethiopia. Forest Ecology and Management 194: 1–10. https://doi.org/10.1016/j.foreco.2004.01.050

Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41: 608–617. https://doi.org/10.1111/j.1744-7429.2009.00517.x

Lin JY, Mo LJ, Zhuang XY, Chen Q, Chen SH, Zhang JF (2006) Niche breadth and overlap of the feeding plants in the forest communities as habitats for *Nomascus Hainanus*. Journal of South China Agricultural University 27: 52–57.

Liu ZH, Zhang YZ, Jiang HS, Southwick CH (1989) Population structure of *Hylobates concolor* in Bawanglin Nature Reserve, Hainan, China. American Journal of Primatology 19: 247–254. https://doi.org/10.1002/ajp.1350190406

Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Paz H, Pérez-García EA, Eunice Romero-Pérez I, Tauro A, Bongers F (2013) Successional changes in functional composition contrast for dry and wet tropical forest. Ecology 94: 1211–1216. https://doi.org/10.1890/12-1850.1

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: Is it generally strong and peaked? Ecology 82: 3479–3492. https://doi.org/10.1890/0012-9658(2001)082[3479:TDDRII]2.0.CO;2

Mammides C, Cords M, Peters MK (2009) Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega forest, Kenya. African Journal of Ecology 47: 87–96. https://doi.10.1111/j.1365-2028.2007.00921.x

Mbora DNM, Meikle DB (2004) Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus (*Procolobus rufomitratus*). Biological Conservation 118: 67–77. https://doi.org/10.1016/j.biocon.2003.07.009

Morgan D, Sanz C (2007) Best practice guidelines for reducing the impact of commercial logging on great apes in western equatorial Africa. IUCN SSC Primate Specialist Group (PSG), Gland, 21–24. https://doi.org/10.2305/IUCN.CH.2007.SSC-OP.34.en

Moscovice LR, Mbago F, Snowdon CT, Huffman MA (2010) Ecological features and ranging patterns at a chimpanzee release site on Rubondo Island, Tanzania. Biological Conservation 143: 2711–2721. https://doi.org/10.1016/j.biocon.2010.07.018

Mwavu EN, Witkowski ETF (2009) Population structure and regeneration of multiple-use tree species in a semi-deciduous African tropical rainforest: implications for primate conservation. Forest Ecology and Management 258: 840–849. https://doi.org/10.1016/j.foreco.2009.03.019

Nagaike T (2002) Differences in plant species diversity between conifer (*Larix kaempferi*) plantations and broad-leaved (*Quercus crispula*) secondary forests in central Japan. Forest Ecology and Management 168: 111–123. https://doi.org/10.1016/S0378-1127(01)00734-4

Olupot W, Chapman CA, Waser PM, Isabirye-Basuta G (1997) Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. American Journal of Primatology 43: 65–78. https://doi.org/10.1002/(SICI)1098-2345(1997)43:1<65::AID-AJP5>3.0.CO;2-W

Pinotti BT, Pagotto CP, Pardini R (2015) Wildlife recovery during tropical forest succession: assessing ecological drivers of community change. Biotropica 47: 765–774. https://doi.org/10.1111/btp.12255

Rode KD, Chapman CA, McDowell LR, Stickler C (2006) Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). Biotropica 38: 625–634. https://doi.org/10.1111/j.1744-7429.2006.00183.x

Sakamaki H, Enari H, Aoi T, Kunisaki T (2011) Winter food abundance for Japanese monkeys in differently aged Japanese cedar plantations in snowy regions. Mammal Study 36: 1–10. https://doi.org/10.3106/041.036.0101

Steininger MK, Hansen M, Townshend JRG, Tucker CJ, Skole D, Defries R (2008) Convincing evidence of tropical forest decline. Proceedings of the National Academy of Sciences of the United States of America 105: e34. https://doi.org/10.1073/pnas.0803707105

Stone R (2011) Last-ditch effort to save embattled ape. Science 331: 390. https://doi.org/10.1126/science.331.6016.390

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http:// www.R-project.org/

Tweheyo M, Lye KA, Weladji RB (2004) Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. Forest Ecology and Management 188: 267–278. https://doi.org/10.1016/j.foreco.2003.07.028

Worman CO, Chapman CA (2006) Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. International Journal of Primatology 27: 203–225. https://doi.org/10.1007/s10764-005-9007-y

Wu W (2007) Hainan black-crested gibbon (*Nomascus sp.cf.nasutus hainanus*) conservation biology status and conservation strategy. PhD Thesis, East China Normal University, Shanghai.

Zang RG, Ding Y, Zhang ZD, Deng FY, Mao PL (2010) Ecological foundation of conservation and restoration for the major functional groups in tropical natural forests on Hainan island. Science Press, Beijing.

Zhang M, Fellowes JR, Jiang X, Wang W, Chan BPL, Ren G, Zhu J (2010) Degradation of tropical forest in Hainan, China, 1991–2008: conservation implications for Hainan gibbon (*Nomascus hainanus*). Biological Conservation 143: 1397–1404. https://doi.org/10.1016/j.biocon.2010.03.014

Zhou J (2008) The ecology and behavior traits of Hainan black-crested Gibbon (*Nomascus hainanus*). PhD Thesis, Northeast Normal University, Changchun.

Zhou J, Wei F, Li M, Zhang JF, Wang D, Pan RL (2005) Hainan black-crested gibbon is headed for extinction. International Journal of Primatology 26: 453–465. https://doi.10.1007/s10764-005-2933-x

Supplementary material 1

Table S1

Authors: Zhi-Dong Zhang, Run-Guo Zang

Data type: species data

Explanation note: Species list, abundances and characteristics of food woody plant species for Hainan gibbon sampled in young natural secondary forests (YSF, < 25 yr since disturbance), middle-aged natural secondary forests (MSF, 25–60 yr since disturbance), old natural forests (OGF, > 60 yr since disturbance) and plantation forests (PF, 20–35 yr) of tropical forest area in BNNR, Hainan Island, China. Tot fts: total number of forest types in which the species occurs.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/natureconservation.31.27407.suppl1